

AFFINITIES AND DISTRIBUTION OF ANTILLEAN ITHOMIIDAE¹

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THE FAMILY ITHOMIIDAE, a characteristic component of the lepidopterous fauna of the American humid tropics, is represented in the Antilles only by two species, both members of the genus *Hymenitis*. One species is found on Cuba, the other occurs on Jamaica and Hispanola (fig. 1), and their affinities are with Central American species. It is surprising that no other species have reached the islands since the lands surrounding the Caribbean support a rich ithomine fauna: it is puzzling to find *Hymenitis*, a genus of frail sun-shunning species, on the Greater Antilles instead of any of the sturdy sun-loving genera. That no ithomine is found on any of the Lesser Antilles is probably because no precisely suitable ecologies are available on those islands.

In order to explore the zoogeographic implications of the Antillean ithomines, it is first necessary to review the systematics and phylogeny of these insects.

SYSTEMATICS

[*Hymenitis* Anonymous, 1807; column 1180. Type of genus, *Papilio polymnia* Linne, 1758, by designation of Hemming, 1934]

Hymenitis Hübner, 1816: 8. Type of genus, *Hymenitis diaphane*: Hübner, 1816, designated by Scudder, 1875.

=*Greta* Hemming, 1934: 28. Type of genus, *Hymenitis diaphane*: Hübner, by original designation.

Hemming's discovery (1934) that *Hymenitis* first appeared in print in 1807, nine years prior to the "Verzeichniss," would seem to reduce the Hübner name to homonymy. By selecting *Papilio polymnia* as type of *Hymenitis* Anonymous, Hemming made the name an absolute synonym for *Mechanitis* Fabricius, 1807; *Greta* was proposed to replace *Hymenitis* Hübner. Hemming's actions were justified under a strict interpretation of the International Code, which provides for the invalidity of anonymous publications only if issued after 1951.

The 1807 article was an unsigned review of a manuscript by Hübner circulated for the information of his colleagues. The anonymous

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Fig. 1. Map of the Caribbean region showing distribution of the Antillean ithomines and related species.

reviewer saw fit to publish the contents of the Hübner manuscript, but with some unauthorized alterations: some of the proposed generic names were replaced, others were juggled. One of the names juggled was *Hymenitis* and the reviewer used it for insects other than those Hübner intended.

The two objections to accepting the validity of this publication are that the generic name *Hymenitis* has no author, and that the unsigned article was malicious and "scooped" Hübner in a manner which today would be condemned as being unethical.

Hemming avers that the review was in fact written by Illiger, the editor of the journal, but there is no proof of authorship in the article itself. At most, Illiger as editor was responsible for permitting an unsigned review to appear, but responsibility and authorship are not the same things. *Hymenitis* Anonymous was the illegitimate offspring of a mother (the editor), but no father (author) was willing to claim it. Proving that Illiger was the author of the review would not purge it either of anonymity or of unethical intent. In my opinion, the first legitimate publication of *Hymenitis* as a generic name was by Hübner, 1816. Hemming could have cleared the situation best by requesting that the 1807 article be suppressed.

HYMENITIS CUBANA

Hymenitis cubana Herrich-Schäffer, 1862: 118. (Cuba).

Figs. 2 and 7

Gundlach (1881) recorded the larval food plant as *galan* (the local name for a member of the genus *Cestrum*, family Solanaceae) and observed that the insect flies slowly and is nearly invisible in the forest shadows. He reported *cubana* from the mountains at each end of the island and said it seemed to be absent from the central Trinidad range; it since has been captured in the central mountains.

Specimens examined, 6 ♂, 12 ♀:

Cuba: Sierra Maestra, Oriente, 1000 feet, 1 ♂, 2 ♀ (M.C.Z.)².
Loma del Gato, Cobra Range, Oriente, 3000 feet, 2 ♂, 4 ♀ (M.C.Z.).
Turquino River, Oriente, 1 ♀ (M.C.Z.). Buenos Aires, Trinidad Mts., 2500-3500 feet, 1 ♂ (M.C.Z.). No station (Oriente, *vide* Bates, 1935), 2 ♂, 5 ♀ (M.C.Z.).

HYMENITIS DIAPHANA

Heretofore known only from Jamaica, a second subspecies from Hispanola is described below. *H. diaphana* is easily distinguished from *H. cubana* because in the former the black marginal band of the forewing follows the wing contour at the apex, while in the latter the black margin is wider and heavier at the apex in males and in females fills

²The following abbreviations are used to indicate museum collections: A.M.N.H., American Museum of Natural History, New York; C.M., Carnegie Museum, Pittsburgh; M.C.Z., Museum of Comparative Zoology, Cambridge.

the entire area beyond the white postdiscal band. Despite these external differences (figs. 2 and 3) the male genitalia of the two species are similar (figs. 7 and 10), though *diaphana* has the saccus, penis and uncus shorter and a different armature at the apex of the valve.

Hymenitis diaphana diaphana (Drury), 1773: 13; pl. 7, fig. 3.
(Jamaica).

Figs. 3 and 10

Drury's figure accurately depicts a male and there can be little doubt of the correct identification. Avinoff and Shoumatoff (1948) comment that *diaphana* is "extremely localized, restricted sometimes to a stretch of land a half-mile across. In such places it is very abundant. It never emerges into the bright sunlight from its dense humid habitat." It is found only in the Blue Mountains of eastern Jamaica at about 3000 feet above sea level.

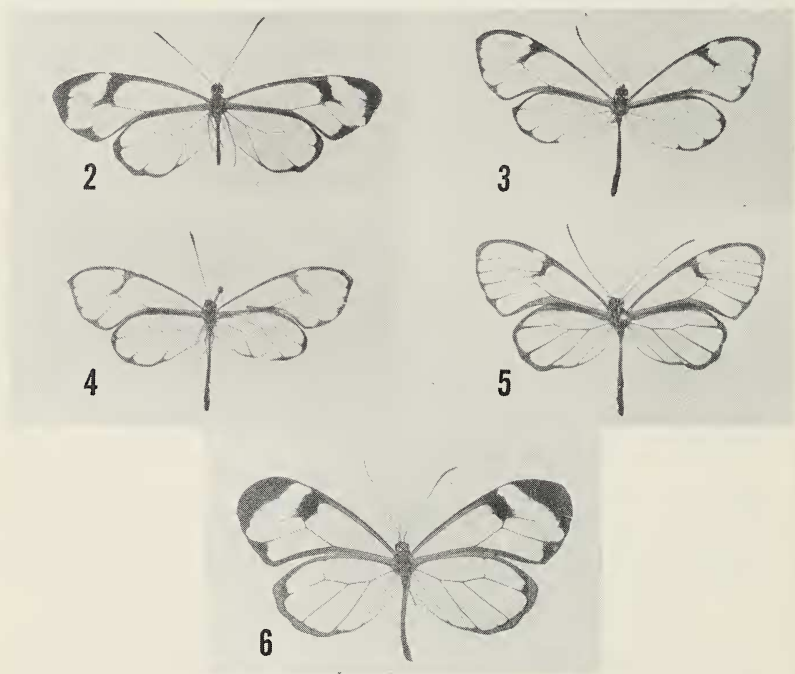


Fig. 2. *Hymenitis cubana*, a male from the Trinidad range, Cuba.

Fig. 3. *H. d. diaphana*, a male from Corn Puss Gap, Blue Mountains, Jamaica.

Fig. 4. *H. d. quisqueya* new subspecies, holotype male from Mt. Diego de Ocampo, Dominican Republic.

Fig. 5. *H. polissena umbrana*, a male from Cachi, near Mt. Irazu, Costa Rica.

Fig. 6. *H. oto*, a male from Mt. Irazu, Costa Rica.

Specimens examined, 74 ♂, 45 ♀:

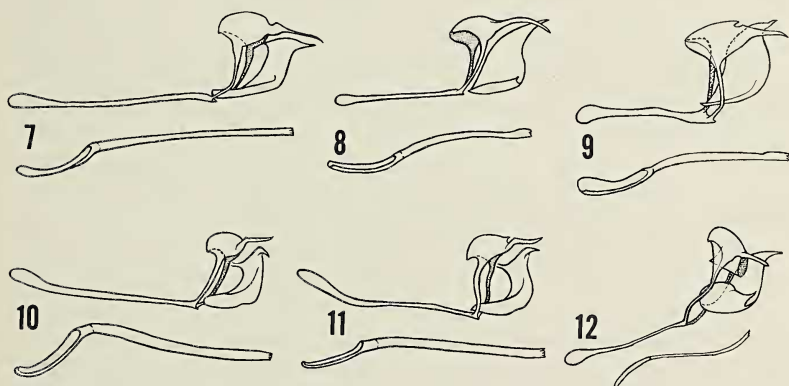
Jamaica: Corn Puss Gap, 37 ♂, 10 ♀ (C. M., M.C.Z.). Cuna Cuna Pass, 31 ♂, 34 ♀ (C.M., M.C.Z.). Fish Brook, 1 ♂, 1 ♀ (C.M.). Moore Town, 2 ♂ (C.M., M.C.Z.). John Crow Hill, 1 ♂ (C.M.). No station, 2 ♂ (A.M.N.H., M.C.Z.).

Hymenitis diaphana quisqueya new subspecies

Figs. 4 and 11

Three males taken by Darlington in the mountains of northwestern Dominican Republic between 3000 and 4000 feet above sea level in July represent an undescribed subspecies and extend the known range of the species to one more island of the Greater Antilles. It is possible that *diaphana* may eventually be found on Puerto Rico.

The Dominican subspecies is similar to *H. d. diaphana* of Jamaica but the following differences are noted in males: The dark discocellular bar of the forewing is narrower and the white costal spot and white scaling on the base of M_1 is only half to two thirds the width of the same markings in *H. d. diaphana*. The black marginal scaling is a little bit wider between M_3 and CU_1 of the forewing and between M_3 and CU_2 of the hindwing, so that this band gives the impression of being of a more uniform width than is true of the Jamaica subspecies. On the underside all dark markings are yellowish brown and appear to be paler than the reddish brown present on *H. d. diaphana*.



Figs. 7 to 12. Male genitalia in lateral view, the left valve removed and the dissected penis below. Fig. 7, *H. cubana*. Fig. 8, *H. oto*. Fig. 9, *H. morgane*. Fig. 10, *H. d. diaphana*. Fig. 11, *H. d. quisqueya* new subspecies, paratype. Fig. 12, *H. polissena umbrana*.

The male genitalia do not differ.

Holotype ♂ and two ♂ paratypes: Mt. Diego de Ocampo, Dominican Republic, 3-4000 feet, July 1938, Darlington. Holotype and one paratype in Museum of Comparative Zoology; one paratype in Carnegie Museum (male genitalia number 1172J).

The ancient indian name for *Hispanola* is said to have been Quisquey.

PHYLOGENY

The coloring and pattern of the wings are difficult to use to associate ithomine subspecies correctly (Fox, 1956) and for that reason must be used with caution to analyze phylogenies. As in many other genera of this family, the wings of *Hymenitis* are mostly transparent and the markings are reduced to the dark marginal bands on both wings, the discocellular band of the forewing and some white scaling beyond the forewing discal cell and faint white spots against the marginal bands. That so many transparent ithomines look so much alike is not part of the "mimicry" phenomenon: transparency is a protective adaptation of the species that live within the shadows of the dense forests.

Study of the Ithomiidae demands close attention to morphologic detail both for correct identification and for phylogenetic analysis. The venation of the hindwings suffices to define most of the genera, but to evaluate the relationships among species of a genus, the male genitalia usually are more useful than wing pattern.

Hymenitis diaphana and *H. cubana* differ from all other members of the genus by the extraordinary length of both the penis and the saccus (figs. 7, 10 and 11). These two species share a simply formed triangular valve with two other species, both Central American, *H. oto* (fig. 8) and *H. morgane* (fig. 9). All other *Hymenitis* species have the sacculus of the valve greatly enlarged and produced posteriorward as a prominent projection which may be quite complex in some. *H. polissena umbrana* Haensch has this development of the sacculus present in a less complex form (fig. 12), and in this respect connects the *diaphana* group with the rest of the genus.

The pattern of *H. cubana*, although so strongly reduced, has one peculiarity of interest: the black marginal band of the forewing is exceedingly thin in Cu_1 - Cu_2 , but wide at the anal angle and above Cu_1 and in females the marginal color fills most of the wing apex beyond the white transverse band. This arrangement of the marginal coloring occurs in only one other species of *Hymenitis*, Central American *oto*. Because of the similarities between *cubana* and *oto* with respect both to male genitalia and to pattern, it is evident that these two species are closely related. Because of certain structural features present in *cubana* and not in *oto* — the length of the penis and saccus in males, and the unique shape of the forewing, which is produced to angles at M_3 and at the apex — *oto* must be the more primitive. This by

no means indicates that *cubana* necessarily evolved from *oto*; it indicates only that the two species were derived from common stock and that *cubana* has become the more specialized, perhaps because its limited geographic range would favor the establishment and preservation of mutations better than the wide range of *oto*.

The residual black markings of *diaphana* are narrowed to a degree matched only by *polissena* of Costa Rica and western Panama (*H. p. umbrana*) and western Ecuador (*H. p. polissena*). Superficially the two species look exactly alike, but in *diaphana* the discocellular veins of the fore wing are displaced distad so that the discal cell is about two thirds of the wing length, while in *polissena* and all other *Hymenitis* the discal cell is only about one half the wing length. Despite the almost exact duplication of pattern between *diaphana* and *polissena*, which certainly cannot be mimicry, the male genitalia differ markedly. Not only is the shape of the valve in *polissena* (fig. 12) more complex, but the penis is of an entirely different shape, being slender, poorly sclerotized and deeply sinuate. *H. polissena* and *diaphana* are not nearly as closely related to each other as are *cubana* and *oto*. The male genitalia of *morgane* (an exclusively Mexican species) are similar to those of *diaphana*, but the patterns on the wings differ greatly.

ZOOGEOGRAPHIC CONSIDERATIONS

The vertebrate fauna of the Greater Antilles seems in general to be related to and derived from the Central American fauna, according to Darlington (1957) and Brown (study in preparation) finds that the butterfly fauna of Jamaica is similarly related; the Antillean Ithomiidae fall into the same pattern. The zoogeographic problem is to ascertain how the fauna of the Antilles got there from Central America and to explain why the South American species are so poorly represented.

For many years it was believed that the Greater Antilles had been physically continuous with Central America until well into Tertiary time and that the existing Antillean fauna was derived, at least in part, from relicts marooned on what became islands when the seas intruded. Schuchert (1935) held this view.

It is no longer believed that when a faunal relationship is shown between two areas separated by seas, such a relationship automatically demonstrates the former existence of a land connection. Simpson (1940, 1953), Darlington (1957) and others have demolished most of the bridges erected by earlier zoogeographers, and only a few such connections are now acceptable. Speculation involving continents drifting about has been put forward in various forms, but continental drift has been used chiefly as a plausible (?) substitute for intercontinental land bridges which otherwise would have had to be discarded.

Animal distribution is generally explained without resort to "Lost Atlantis" or to continental drift. Matthew's theory (1915) of holarctic distribution accounts adequately for the presence of living faunae on all continents and islands; within the framework of Matthew's theory, rafting accounts for much of the dispersal to islands. The term "rafting" may be taken in a general sense, comprising transportation by literal rafts, by aerial means and by "hitch hiking."

Rafts of flotsam, formed in flooded rivers and drifting out to sea, carry many animals. Should such a raft happen to find its way to an island, the surviving individuals could disembark and establish themselves in a new habitat. Transportation by aerial means is well known for spiders and occurs in many other groups, especially for small, light weight arthropods. The power of flight combined with air currents may carry somewhat larger species for great distances. Hitch hiking is usual for arthropods with parasitic or semiparasitic habits.

The hazards involved in rafting by any means are such that the chances of a successful journey — one leading to a new colony of the species — are small indeed, and the hazards are especially great in the flotsam rafts. Flotsam rafts normally break apart at the mouth of the river and at sea they are likely to be well doused by salt water even if no storm is encountered. Should rafted individuals survive exposure and the vagaries of wind and current happen to put them ashore, the landing must be made at or very near a suitable ecological situation. It has been pointed out that, despite the poor probabilities, a successful trip need occur but once during a very long period of time and it is not difficult to demonstrate mathematically that fortuitous if improbable conditions might pertain occasionally. If the animal being rafted is physiologically able to survive exposure to salt water, or if its habits are such that it may travel in some protected part of the raft, there is a better chance of a successful journey. Presumably most mammals, for example, need only to cling to the flotsam until a landing is made and during the trip they would face a greater hazard from starvation or exposure to sun than from salt water; the larvae of wood-boring insects might be transported safely within their burrows. Conversely, animals without physiological protection against exposure and without habits that would place them in a protected situation *en route*, have a lessened probability for survival.

Transportation by flotsam rafts appears to be out of the question for *Hymenitis*. Salt water would destroy eggs, larvae, pupae or adults and none of these stages is passed in a protected place. Because *Hymenitis* requires a very specific ecological situation, one which is not present near the Antillean coasts, no mathematical calculation of the chances of survival for a long enough time to reach an island has any bearing. If not destroyed by the sea, these insects would still face an overland journey of many miles in order to reach forests 3000 feet above sea level. Furthermore, it seems implausible that ocean currents

or the winds (fig. 1) could give much assistance to transporting Central American butterflies to the Antilles.

Aerial transportation also is unlikely in the case of *Hymenitis*, though it cannot be ruled out as a mode of dispersal for other butterflies. Unlike most groups, *Hymenitis* remains within the cover of dense forest and does not seek the sun or open places; the reaction to the least breeze is to drop to the ground and cling. It is conceivable that a hurricane could transport adults, provided the wind were strong enough to suck the insects out of the forest, but not only is the direction of winds toward, not from Central America, but it is hard to imagine that such wind force would not also crush and kill the insects.

If rafting by any method could serve to distribute *Hymenitis* or the other ithomines, one would expect on the Greater Antilles to find representatives of the rich fauna of Colombia, Venezuela and the Guianas rather than of the reduced fauna of Central America, since all factors of wind and current are favorable to rafting from the northern coast of South America but unfavorable to rafting from Central America. Of all the ithomines, *Hymenitis* and other groups with similar habits are the most unlikely to be rafted. If rafting occurred, why are the sun-loving *Mechanitis*, *Melinaea*, *Tithorea* and *Hypothyris* not present on the Antilles?

Darlington (1957) comments, "It might be supposed that the Gulf Stream would prevent drift from reaching the West Indies from Central America and might favor drift transport from South America in spite of the greater distance. But this plausible idea is not supported by facts." I must agree with his view on this matter, but for a reason different than he expressed it. For Ithomiidae there are no facts to support drift (rafting) by any method.

The Greater Antilles stand within the continental shelf, separated from Central America only by shallow seas, and the possibility cannot be dismissed that the two present land areas were once continuous. Such a connection would not be "Lost Atlantis" bridging the deep seas and while there is little evidence to support the connection, there is no geologic evidence against it. Darlington (1957) assumed that the Greater Antilles were formed by oceanic volcanoes because volcanic rocks and marine limestones are present. Woodring (1954), however, commended that, "It is quite evident on ordinary geological grounds that a considerable part of the Caribbean Sea was land during the Cretaceous and that at least some of this land was still land during the Eocene." F. M. Brown (private communication) states that current geologic and oceanographic investigations, partly conducted by private industry and not yet published, are yielding data which seem to indicate that the Greater Antilles were indeed once connected with Central America. At present, the entire question should be regarded without prejudice as an open one.

Schuchert (1935) thought that the Greater Antilles were connected by dry land with Central America along what is now the Nicaraguan swell — a high, wide hump of the sea floor running from Puerto Rico, Hispanola and Jamaica to Honduras and Nicaragua — and by a similar connection between Yucatan and western Cuba. He suggested that the entire island group was part of the Central American mass as recently as the Oligocene and that during Miocene time Jamaica, Hispanola and Puerto Rico were connected sporadically with the continent but that Cuba remained insular. Perhaps Schuchert was right.

Proponents of rafting have a second line of defense: the belief that only the geography and climates of late Pliocene and of Pleistocene times exerted significant influence on the distribution of modern faunae. This belief is based on study of vertebrates, and nothing in the present paper is intended as contradictory to the conclusions of students of that phylum. The enviably full fossil record has permitted mammalogists to reconstruct a reasonably complete picture of mammalian evolution during the Tertiary. Oligocene time, for example, need not be considered in connection with the distribution of most mammals, since modern mammal species were not yet in existence.

Zoogeographers working with invertebrates, particularly with groups like Lepidoptera for which there is almost no significant fossil record, must rely upon principles of evolution and zoogeography developed by mammalogists. "The fundamentals of invertebrate distribution are substantially the same as those affecting vertebrates . . . The salient difference is timing" (Miskimen, 1961). Jeannel (1949) pointed out that, "the antiquity of insects becomes evident when compared with that of vertebrate groups. The Tertiary and Quaternary lasted for 30 million years³ and comprised the entire evolution of the placental mammals; but at the beginning of the Tertiary, most insect genera already existed much as they do today." According to Vandel (1949), "The most evolved orders of insects (Lepidoptera, Diptera, Hymenoptera) made their appearance during the Mesozoic epoch. At the beginning of the Tertiary, the living entomological fauna [of the world] was definitely constituted and thereafter underwent no important alteration." To evaluate insect distribution it is necessary to consider events of the entire Tertiary, not just the effects of recent glaciations.

There is no doubt that the insect fauna of the north temperate zone was profoundly affected by Pleistocene glaciation: the extent of influence of glaciation on tropical and subtropical faunae is less clear and in many regions may have been negligible. In all situations there is a basic difference between the effect of the Pleistocene upon mammals and its effect upon insects: mammals were evolving, insects had already evolved modern genera and species. Recent glaciation superimposed certain geographic adjustments on pre-existing distributional patterns of insects, but created the distributional patterns of modern mammals.

³Today we know the time estimate should be much longer.

The Ithomiidae is one of the most primitive families of the Nymphaloidae (Fox, 1956) and must be of considerable antiquity. The fact that one genus (*Tellervo*) is found in the East Indies while the rest are neotropical suggests that the family must have been in existence at the opening of the Tertiary. Even though *Hymenitis* is one of the more specialized genera of the family, it probably was in existence in Oligocene time. Thus if Schuchert's connection between the Greater Antilles and Central America during Oligocene or Miocene actually existed, it would have provided a distributional route to the Greater Antilles for these butterflies.

An objection to land route distribution — the same objection that arises to rafting — is the question of why only certain *Hymenitis* species are found on the islands. This is a question which cannot be answered definitely, no matter which method of dispersal is postulated, but it is easier to imagine that *Hymenitis* managed to survive while other genera became extinct than it is to imagine that *Hymenitis* alone of all the ithomines managed to beat the odds and find its way to the islands from Central America.

SUMMARY

1. The only Ithomiidae found on the Antilles are *Hymenitis cubana* on Cuba, *H. d. diaphana* on Jamaica and *H. d. quisqueya* (herein described) on Hispanola.

2. The affinities of these Antillean ithomines are with certain Central American *Hymenitis*. All are transparent-winged inhabitants of the humid forests, shunning sunlight and open situations; all are found from 1000 to 7000 feet above sea level.

3. Distribution by rafting is unlikely because of the direction of sea and air currents and because of the habits and fragility of *Hymenitis*. If rafting ever distributed ithomines, the fauna of Venezuela and the Guianas and the hardier sun-loving should be represented on the islands.

4. Alternatively, these ithomines may have reached the Antilles during early Tertiary time if, as Schuchert and others thought, the islands once were continuous with Central America.

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